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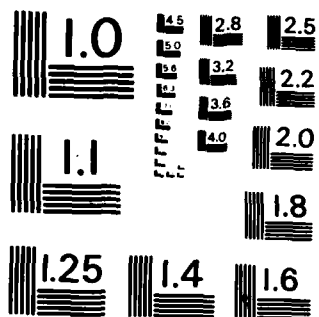
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AN ANALOG MODEL OF COMPUTATION FOR  
THE ILL-POSED PROBLEMS OF EARLY VISION

Tomaso Poggio and Christof Koch

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A large gap exists at present between computational theories of vision and their possible implementation in neural hardware. The model of computation provided by the digital computer is clearly unsatisfactory for the neurobiologist, given the increasing evidence that neurons are complex devices, very different from simple digital switches. It is especially difficult to imagine how networks of neurons may solve the equations involved in vision algorithms in a way similar to digital computers. In this paper, we suggest an analog model of computation in electrical or chemical networks for a large class of vision problems, that maps more easily into biologically plausible mechanisms. Poggio and Torre (1984) have recently recognized that early vision problems such as motion analysis (Horn and Schunck, 1981; Hildreth, 1984a,b), edge detection (Torre and Poggio, 1984), surface interpolation (Grimson, 1981; Terzopoulos 1984), shape-from-shading (Ikeuchi and Horn, 1981) and stereomatching can be characterized as mathematically ill-posed problems, in the sense of Hadamard (1923). Ill-posed problems can be "solved", according to regularization theories, by variational principles of a specific type. A natural way of implementing variational problems are electrical, chemical or neuronal networks. We present specific networks for solving several low-level vision problems, such as the computation of visual motion and edge detection.

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### III-Posed Problems and Variational Principles

In mathematical analysis ill posed problems are defined as such problems that do not have a unique solution that depends continuously on the data. Early vision problems are ill-posed, typically because the solution is either not uniquely constrained by, or does not depend continuously on the data. Computation of the velocity field and the recovery of shape from shading are examples of the first type; edge detection, considered as the problem of measuring spatial changes of intensity in an image, is an example of the second class. Rigorous regularization theories for "solving" ill-posed problems have been developed in recent years (see especially Tikhonov and Arsenin, 1977; and Nashed, 1974). Ill-posed problems of the form

$$y = Az, \quad (1)$$

where  $A$  is a possibly nonlinear operator on the unknown solution  $z$ , and  $y$  is the data, can be regularized by introducing suitable norms  $\|\cdot\|$ , usually quadratic, and a "stabilizing" functional  $\|Pz\|$ , with certain mathematical properties. Its exact form depends on the physical constraints that are relevant to the specific problem. The regularized solution is then obtained in terms of a variational principle. For simplicity, we consider here two main methods (the second and third methods in Poggio and Torre, 1984):

(a) If the data are exact, then the regularized solution  $z$  is the function that minimizes

$$\|Pz\| \quad (2)$$

among the  $z$  such that  $y = Az$ .

(b) If the data are not exact, the regularized solution is  $z$  that minimizes

$$\|Az - y\|^2 + \lambda \|Pz\|^2 \quad (3)$$

where  $\lambda$  is a regularizing parameter (see Poggio and Torre, 1984).

Typically,  $A$  and  $P$  are linear operators and  $P$  usually corresponds to a physically relevant smoothness constraint. Poggio and Torre (1984) have argued that most early vision problems can be solved in terms of variational formulations of this type. A few such solutions have been already obtained. A representative example is the computation of the velocity field (Hildreth, 1984a,b; see also Poggio and Torre, 1984; for a second example see Poggio, Voorhees and Yuille, 1984)<sup>1</sup>. In this case the velocity  $V$  of each point along a curve in the image is underdetermined, since

$$V(s) = v^T(s)T(s) + v^\perp(s)N(s) \quad (4)$$

( $T$ ,  $N$  are the unit vector tangent and perpendicular to the contour respectively,  $s$  is the arc length), and only  $v^T(s)$  can be obtained by local measurements, if the curve is smooth. The stabilizing functional derived by physical considerations (Hildreth, 1984a,b) is obtained from  $PV = \partial V / \partial s$ . The regularized solution is found by

(a) minimizing

$$\left\| \frac{\partial V}{\partial s} \right\|^2 = \int \left( \frac{\partial V}{\partial s} \right)^2 ds \quad (5)$$

subject to the data  $V^T$ , if the data are exact, or by

(b) minimizing

$$\|V^T - V \cdot T\|^2 + \lambda \left\| \frac{\partial V}{\partial s} \right\|^2, \quad (6)$$

where  $\lambda^{-1}$  is a weighting factor expressing the reliability of the velocity measurements<sup>2</sup>, when the data are affected by errors.

### Analog Networks for Solving Variational Problems

As suggested by Terzopoulos (1984), analog networks—chemical, electrical or mechanical—are a natural computational model for solving variational principles. We know from physics that the behavior of such systems, in fact the behavior of any physical system, can be described using variational principles (MacFarlane, 1970). In the frictionless world of classical mechanics a system's state variables will behave in such a way as to minimize the associated Lagrangian. Electrical network representations have been constructed for practically all of the field equations of physics — many of them are equivalent to variational principles (for an electrical network implementation of Schrödinger's equation see Kron, 1945). A fundamental reason for a natural mapping between variational principles and electrical or chemical networks is Hamilton's Least Action principle<sup>3</sup>. The class of variational principles that can be computed by analog networks is dictated by Kirchhoff's current and voltage laws (KCL and KVL), which simply represent conservation and continuity restrictions satisfied by each network component (appropriate variables are usually voltage and current for electrical networks and affinity, i.e. chemical potential, and chemical turnover rate for chemical systems). KCL and KVL provide the unifying structure of network theory. A large body of theoretical results is available about networks satisfying them, including classical thermodynamics (Oster, Perelson and Katchalsky, 1971). In particular, KCL and KVL imply Tellegen's theorem<sup>4</sup>. For a network containing only sources and linear resistors, Tellegen's theorem implies Maxwell's minimum heat theorem: *the distribution of voltages and currents is such that it minimizes the total power dissipated as heat*<sup>5</sup>. These results can be extended to nonlinear circuit components<sup>6</sup> (MacFarlane, 1970; Oster & Desoer, 1971), but in the following we will restrict ourselves to linear resistors. Since the power dissipated as heat by linear resistors is a quadratic functional of the form

$$\sum_k I_k V_k \quad (7)$$

where  $I_k$  and  $V_k$  are the current and the voltage respectively, and the sum is taken over all resistive processes  $r_k$ , it follows that any network consisting of linear resistors and voltage sources  $E_k$  has the following associated quadratic functional that is minimized

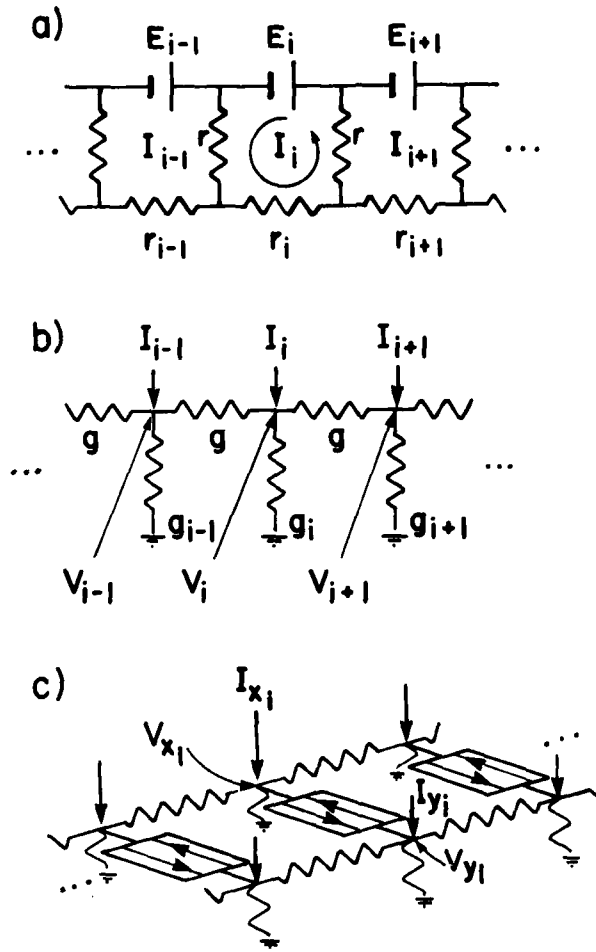
$$\sum_k r_k I_k^2 - \sum_i E_i I_i \quad (8)$$

where the second sum includes all the batteries. The functional for the network containing current sources is very similar<sup>7</sup>.

It is then easy to show formally that electrical networks of linear resistors and batteries (or current sources) can solve quadratic minimization problems in a Hilbert space<sup>8</sup>. The corresponding linear equations  $Qz = b$  have a unique solution  $z$ , corresponding to the unique solution of the variational principle. Interestingly, the data  $b$  can always be represented in terms of current or voltage sources. The matrix  $Q$  is the symmetric, real matrix of the network resistances<sup>9</sup>.

A simpler argument also shows that variational principles of the type of equation (2) and (3) can be solved by linear networks. The Euler-Lagrange equations associated with

equations (2) and (3) are linear in  $z$ . In the discrete case, they correspond to  $n$  linear, coupled algebraic equations that can be solved by networks of passive, linear resistors and voltage/current sources<sup>9</sup>. An alternative implementation, common on analog computers, involves operational amplifiers (Jackson, 1960). As pointed out by Terzopoulos in the context of vision (earlier, Horn (1974) proposed an analog implementation of the lightness computation), a significant advantage of an analog implementation is its extreme parallelism and speed of convergence. Another advantage of resistance networks is their robustness against random errors in the resistance units of the network (Terzopoulos, 1984; Karplus, 1958). A disadvantage is the limited precision of the analog signals.



**Figure 1:** Three resistive networks computing the smoothest velocity field solution of Hildreth, 1984a. The first two networks correspond to the situation where the constraints imposed by the data are to be satisfied exactly. The equation for the current, which corresponds to the desired  $v^T$  in mesh  $i$  (for figure 1a), is given by  $(2r + r_i)I_i - rI_{i+1} - rI_{i-1} = E_i$ , where the value of the battery  $E_i$  depends on the velocity data  $v^T$  at location  $i$ . The voltage at node  $i$ , corresponding to  $v_i^T$ , for the network 1b, the dual of network 1a, is given by  $(2g + g_i)V_i - gV_{i+1} - gV_{i-1} = I_i$ , where the injected current  $I_i$  depends on the velocity data. Sampling the voltage between nodes corresponds to linear interpolation between the node values. Network 1c, consisting of two interconnected networks of the type shown in 1b, solves the velocity field problem when the data are not exact. The equations for the  $i$ -th nodes are  $(2g_x + g_{x_i})V_{x_i} - g_x V_{x_{i+1}} - g_x V_{x_{i-1}} + c_i V_{y_i} = d_{x_i}$  and  $(2g_y + g_{y_i})V_{y_i} - g_y V_{y_{i+1}} - g_y V_{y_{i-1}} + c_i V_{x_i} = d_{y_i}$ . However, unlike the two purely passive networks shown above, an active element may be required, since the cross-term  $c_i$ , relating the  $x$  and the  $y$  components of velocity, can be negative. Such a negative resistance can be mimicked by operational amplifiers.

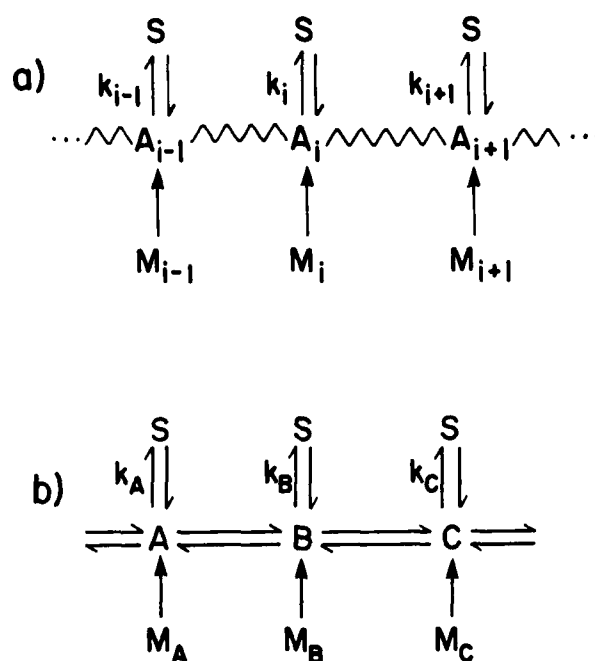


## An Example: Circuits for the Velocity Field Computation

We will consider next some specific networks for solving the optical flow computation<sup>10</sup>. The simpler case is when the measurements of the perpendicular component of the velocity,  $v_i^\perp$ , at  $n$  points along the contours are exact. In this case, the discretized Euler-Lagrange equations, corresponding to the regularization solution, equation (5), are (Hildreth, 1984a)

$$(2 + \kappa_i^2)v_i^\top - v_{i+1}^\top - v_{i-1}^\top = d_i, \quad (9)$$

where  $\kappa$  is the curvature of the curve at location  $i$ ,  $d_i$  is a function of the data  $v_i^\perp$  and the curve and  $v_i^\top$  is the unknown tangential component of the velocity  $v_i$  at location  $i$  to be computed. Figure 1a and 1b shows two simple networks that solve equation (9), where one network is the dual of the other.



**Figure 2:** Two examples of chemical networks solving the motion problem for exact measurements. They are equivalent, under steady-state conditions, to the electric circuit of figure 1b. Fig. 2a illustrates a diffusion-reaction system. A substance  $A$  (the concentration of which corresponds to the desired  $v^\top$ ) diffuses along a cable while reacting with an extracellular substance  $S$  (first order kinetics). The corresponding On-rate  $k_i$  varies from location to location. This could be achieved by a differential concentration of an enzyme catalysing the reaction or by varying the properties of the membrane where the reaction has to take place. The Off-rates can be either constant or vary with location. The inputs are given by the influxes of substance  $A$ . Figure 2b shows an instance of a lumped chemical network.  $n$  different, well-mixed substances, interact with each other and with the substrate  $S$ . Assuming first-order kinetics, these reactions can mimic a linear resistance under steady-state conditions. The input is given by the influx  $M_X$  and the output by the concentration of  $X$ . Chemical networks of this type are a kind of *computational soup*.

The equation describing the  $i$ -th node, in the case of figure 1b, is

$$(2g + g_i)V_i - gV_{i+1} - gV_{i-1} = I_i \quad (10)$$

where  $V_i$  is the voltage—corresponding to the unknown  $v_i^T$ —and  $I_i$  the injected current at node  $i$ —corresponding to the measurements  $v_i^L$ . It is important and surprising that this implementation does not require negative resistances. When the constraints are satisfied only approximately (equation (6)), the equations are

$$\begin{aligned} (2 + b_{x_i}^2)V_{x_i} - V_{x_{i+1}} - V_{x_{i-1}} + c_i V_{y_i} &= d_{x_i} \\ (2 + b_{y_i}^2)V_{y_i} - V_{y_{i+1}} - V_{y_{i-1}} + c_i V_{x_i} &= d_{y_i} \end{aligned} \quad (11)$$

where  $b_i$  depends on the contour and  $V_{x_i}$  and  $V_{y_i}$  denote the  $x$  and  $y$  component of the unknown velocity  $v_i$  at location  $i$ . The corresponding network is shown in Figure 1c. The resistances  $c_i$ , however, can be either positive or negative, and may therefore require active components such as operational amplifiers<sup>11</sup>. In the limit, as the meshes of the circuit become infinitesimally small, the network solves the continuous variational problem, and not simply its discrete approximation.

We have devised similar analog networks for solving other variational problems arising from regularization analysis of several early vision problems such as edge detection (Poggio *et al.*, 1984) and surface interpolation<sup>12</sup> (Terzopoulos, 1984). These networks are analog solutions to certain kinds of spline interpolation and approximation problems. For instance, in the case of surface interpolation the analog network solves the *biharmonic* equation which is the Euler-Lagrange equation corresponding to the variational problem associated with thin-plate splines. The stabilizing functionals used in regularization analysis of vision problems typically lead to local and limited connections between the components of the network.

### Solving Ill-Posed Problems with Biological Hardware

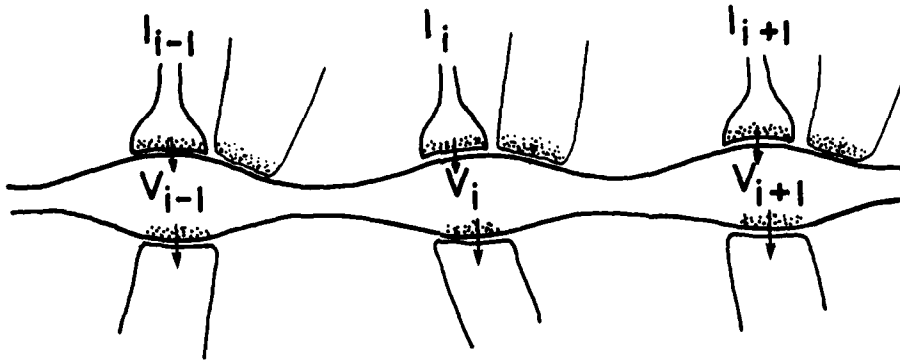
The mathematical property of ill-posedness determines a common computational structure for the solution to specific problems in early vision based on variational principles of a specific type. Analog electrical networks are a natural hardware for computing such variational principles. Because of the well-known isomorphism between electrical and chemical networks (see for instance Busse and Hess, 1973 or Eigen, 1974) that derives from the common underlying mathematical structure, appropriate sets of chemical reactions can be devised, at least in principle, to "simulate" exactly the electrical circuits. Fig. 2 shows two chemical networks that are equivalent (in the steady state) to the electrical circuit of fig. 1b<sup>13</sup>.

Electrical and chemical systems of this type therefore offer a computational model for early vision that is quite different from the digital computer. Equations are "solved" in an implicit way, exploiting the physical constraints provided by Kirchhoff's laws. It is not difficult to imagine how this model of computation could be extended to mixed electrochemical systems by the use of transducers, such as chemical synapses, that can decouple two parts of a system, similarly to operational amplifiers<sup>14</sup>.

Could neural hardware exploit this model of computation? Increasing evidence shows that electrotonic potentials play a primary role in many neurons (Schmitt, Dev and Smith, 1976) and that membrane properties such as resistance, capacitance and equivalent inductance (arising through voltage and time-dependent conductances; see for instance Cole, 1968 and Koch, 1984) may be effectively modulated by various types of neurotransmitters, acting over very different time scales (Marder, 1984). Dendrodendritic synapses and electrical gap junctions serve to mediate graded, analog interactions between neurons and do

not rely on all-or-none spikes (Graubard and Calvin, 1976). Such an electrical mediated interaction between cells has been exploited in a model of the small-signal behavior of the photoreceptor network in the vertebrate retina (Torre and Owen, 1983).

When implementing electrical networks in equivalent neuronal hardware, one can draw upon a large number of elementary circuit elements<sup>1,3</sup> (Fig. 3). Patches of neuronal membrane or cytoplasm can be treated as resistance and capacitance. Voltage sources can be mimicked by synapses on dendritic spines (Koch and Poggio, 1983), whereas synapses on large dendrites act as current sources. Chemical synapses could effectively serve to decouple different parts of a network. Chemical processes such as the reactions associated with postsynaptic effects or with peptides could also be thought as part of a complex electrochemical network. Obviously, the analogy cannot be taken too literally. It would be very surprising to find the exact neural analog of the circuit of Fig. 3 somewhere in the CNS. We are convinced, however, that the *style* of computation represented by analog circuits represents a very useful model for neural computations as well as a challenge for future VLSI circuit designs.



**Figure 3:** This schematic figure illustrates an hypothetical neuronal implementation of the regularization solution to the motion problem. A dendrite, acting both as pre- and post-synaptic element has a membrane resistance that can vary with location. It can implement under steady-state conditions the circuit 1b. The inputs—corresponding to the measurements  $v^\perp$ —are given by synaptic mediated current injections, while the output voltages—corresponding to the desired  $v^\top$ —are sampled by dendro-dendritic synapses. The membrane resistance can be locally controlled by suitable synaptic inputs—corresponding to the curvature of the contour—from additional synapses opening channels with a reversal potential close to the resting potential of the dendrite. This scheme can easily be extended to the case where the measurements of the perpendicular velocities are not exact, by having a similar, second dendrite (see also figure 1c). The interaction between both dendrites takes place via two reciprocal chemical synapses. If the corresponding cross-term in equation (11) is negative, the chemical synapse must be inverting, presynaptic depolarization leading to an hyperpolarization.

The regularization approach is not limited to early vision. Other sensory modalities and motor control can be analyzed in a similar way (Poggio and Torre, 1984). For instance, the network corresponding to the variational principle suggested by Hogan for controlling the formation of voluntary movements (Hogan, 1984) is topologically related to the electrical network underlying one-dimensional edge detection.

The variational principles that we have considered so far for early vision processes are

quadratic and therefore lead to linear networks. This is not always to be expected. The ill-posed problem of combining several different sources of surface information, for instance, may lead to non-quadratic regularization expressions and to corresponding nonlinear networks. Though this is a topic that still needs to be explored, nonlinearities may greatly expand the rather restricted universe of computations that can be performed in terms of quadratic minimization principles (Hopfield, 1984). Again, analog networks may be used to solve these minimization problems, that will in general have multiple local minima corresponding to the zeros of the *mixed potential* (Brayton and Moser, 1964; Oster, Perelson and Katchalsky, 1973). Schemes similar to annealing (Metropolis, Rosenbluth, Rosenbluth, Teller and Teller, 1953; Kirkpatrick, Gelatt and Vecchi, 1983; Hinton and Sejnowski, 1983) may be easily implemented by appropriate sources of gaussian noise<sup>15</sup>. In a chemical network "noise" may be introduced in various, simple ways. Needless to say, a number of biophysical mechanisms, such as somatic and dendritic spikes, interactions between conductance changes, voltage and time-dependent conductances etc., are likely to be used by neurons and patches of membrane to perform a variety of nonlinear operations.

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## Footnotes

[1] In 1-D the problem of edge detection is considered as a problem in numerical differentiation of the light intensity  $f(x)$ . Numerical differentiation can be regularized in the following way. The model is  $y_i = f(x_i)$ . We want to estimate  $f'$ . We chose a regularizing functional  $\|f'\| = \int (f''(x))^2 dx$ , where  $f''$  is the second derivative of  $f$ .

The solution can be found by

(a) minimizing

$$\int [f'']^2 dx \quad (1.1)$$

subject to the data  $y_i$ , or by

(b) minimizing

$$\sum (y_i - f(x_i))^2 + \lambda \int [f''(x)]^2 dx \quad (1.2)$$

and then in either case by differentiating  $f$  to obtain  $f'$ .

[2] Regularization theory provides techniques to determine the best  $\lambda$  (Tikhonov and Arsenin, 1977; see also Reinsch, 1967). For instance, methods such as the Generalized Cross Validation method (Wahba, 1980) may be used to find the optimal  $\lambda$ . In the case of edge detection  $\lambda$  effectively corresponds to the scale of the filter (Poggio *et al.*, 1984).

[3] The main form of Hamilton's Postulate of least action states that the motion of a dissipation-less dynamical system, free from external disturbance, from a configuration at time  $t_1$  to another configuration at time  $t_2$ , is such that the integral of its Lagrangian  $L = T - U$  is stationary on the path followed. That is

$$\int_{t_1}^{t_2} L dt = \text{Extremum.}$$

If one extends Hamilton's Postulate to dissipative systems acting under external forces it can be shown that

$$\int_{t_1}^{t_2} (L + W) dt = \text{Extremum}$$

must hold, where  $W$  is the virtual work done by the dissipative elements (e.g. resistors) and the sources.

[4] Kirchhoff's laws are physical restatements of the topological properties of the dynamic space. For electrical networks they correspond to conservation of flows (KCL) and uniqueness of potential (KVL). Tellegen's theorem capture the basic constraints provided by KCL and KVL. It is one of the most general and powerful results of network theory and is independent of any assumption about constitutive relations or stationarity.

*Tellegen's theorem:* If  $U$  is the vector of branch potentials (a component for each branch) and  $J$  is the vector of branch flows, then

$$U^T J = 0.$$

Thus the flow and the potential variables are orthogonal at any instant in time.

[5] If one assumes the electric circuit to be isothermal, then dividing the heat,  $Q$ , dissipated in the resistors by the temperature  $T$ , we find that  $Q/T = dS/dt$  is also minimum (Oster and Desoer, 1971). The theorem of minimum entropy production expresses a kind of variational property of linear nonequilibrium systems. When given boundary conditions prevent the system from reaching thermodynamic equilibrium (i.e. zero entropy production) the system settles down in the state of "least dissipation" (Prigogine, 1967).

[6] In addition to Hamilton's Postulate, there are two specialized variational principles for networks composed entirely of sources and linear or nonlinear dissipative elements. In such a network, the actual distribution of the currents will be such as to minimize the total content  $G$  of the system where  $G$  is given by

$$G = \int_0^I v di.$$

Conversely, the distribution of voltages will be such as to minimize the total co-content  $J$  of the system where

$$J = \int_0^V i dv.$$

If the network considered contains only linear resistors and sources, then both of the above principles reduce to Maxwell's Stationary Heat Theorem: the distribution of voltages and currents will be such as to minimize the total power dissipated as heat (MacFarlane, 1970).

[7] In a network of linear resistances  $r_k = 1/g_k$  and current sources  $I_i$  the associated quadratic power functional to be minimized is given by

$$\sum_k g_k V_k^2 - \sum_i I_i V_i,$$

where the second sum includes all the current sources.

[8] Assume a Hilbert space with an inner product  $\langle \cdot, \cdot \rangle$ , which defines a quadratic norm  $\|\cdot\|$ . An ill-posed problem can be formulated in terms of norms; i.e. minimize

$$\|Pz\|^2 + \lambda \|Az - b\|^2 \quad (8.1)$$

where  $P$  is any linear operator and  $b$  is the data. This is the third regularization method in Poggio and Torre (1984). Writing this in terms of inner products, we have

$$\langle Pz, Pz \rangle + \lambda \langle \Lambda z - b, \Lambda z - b \rangle. \quad (8.2)$$

This is equal to

$$\langle Pz, Pz \rangle + \lambda \langle \Lambda z, \Lambda z \rangle - \lambda \langle \Lambda z, b \rangle - \lambda \langle b, \Lambda z \rangle + \lambda \langle b, b \rangle \quad (8.3)$$

Since the last term is constant, it can be disregarded in the minimization. If the adjoints of the operators  $P$  and  $\Lambda$  are denoted by  $P^*$  and  $\Lambda^*$  respectively, minimizing this expression is equivalent to minimizing

$$\langle z, P^* P z \rangle + \lambda \langle z, \Lambda^* \Lambda z \rangle - 2\lambda \langle z, \Lambda^* b \rangle. \quad (8.4)$$

Defining a new operator  $Q$  by  $Q = P^* P + \lambda \Lambda^* \Lambda$ , we can formulate the original variational problem as the problem of minimizing

$$\langle z, Qz \rangle + \lambda' \langle z, \Lambda^* b \rangle \quad (8.5)$$

The first term can be identified with the total power dissipated in a linear resistive network, while the second term is the voltage- or current-source contribution. Note that  $Q$  is automatically self-adjoint. If  $Q$  is a linear operator satisfying

$$m \langle z, z \rangle \leq \langle z, Qz \rangle \leq M \langle z, z \rangle$$

for all  $z \in H$ , with  $H$  being a Hilbert space, and some  $M, m > 0$ , the vector  $z$  minimizing eq.(8.5) is the unique solution of the equation  $Qz = b$  (thus the energy inner product  $\langle z, Qz \rangle$  is H-elliptic and bounded, see Terzopoulos, 1984). The problem of minimizing the quadratic functional on a Hilbert space can be formulated as a Hilbert space minimum norm problem (Luenberger, 1969).

[9] Let the Euler-Lagrange equations associated with a quadratic variational problems be  $Qz = b$ , where the  $n$ -dimensional vector  $b$  is a function of the data. These equations can be implemented in a planar network containing only linear resistances and voltage sources. For every variable  $z_i$  one mesh is set up (with the associated mesh current  $I_i$ ). The mesh consists of a battery  $E_i$  and a resistance  $r_{ij} = q_{ij}$  for every non-zero entry in the  $i$ -th row of  $Q$ . Moreover, a very simple auxiliary circuit connects the  $i$ -th and the  $j$ -th mesh via an auxiliary resistance  $R_{ij}$ . The associated circuit current flows not only through  $R_{ij}$ , but also through  $r_{ij}$  of the  $i$ -th mesh and  $r_{ji}$  of the  $j$ -th mesh. However, since this scheme requires up to  $n^2/2$  resistances, it seems only feasible if  $Q$  is sparse. Fortunately, the operator  $P$  used in the variational problems of early vision (Poggio and Torre, 1984) has a small and limited support, so that the corresponding matrix  $Q$  will have very few non-zero entries. Although this procedure will always yield an electrical network with linear elements implementing  $Qz = b$ , its physical realization might require negative resistances (if the corresponding term in  $Q$  is negative), which need to be mimicked by active elements<sup>11</sup>. Alternatively, one can use the signal-flow graph techniques of Mason and Coates for solving linear algebraic equations (Kuo, 1967).

[10] S.Ullman (pers. comm.) has suggested an analog mechanical spring model for the computation of the smoothest velocity field. Minimization of the potential energy contained in the springs corresponds to minimization of equation (5) directly in velocity space. It

has proved so far impossible to map this very special model into electrical or chemical networks.

[11] Physically realizable linear resistances, whether in electrical or in chemical systems, must dissipate energy, i.e. they are constrained to the upper right and the lower left quadrant in the  $I-V$  plane and can thus only be positive. However, there are at least three different options for implementing negative resistances using basic circuit components. (i) The positive and negative resistances can be replaced in a purely resistive network by inductances and capacitances, with impedance  $i\omega L$  and  $-i/(\omega C)$  respectively. The network equations are then formulated in terms of the currents and voltages at the fixed frequency  $\omega$ . (ii) The negative resistance can be implemented by the use of operational amplifiers or similar active circuit elements. A case in point are reciprocal inhibitory synapses, like those found between mitral and granule cells in the mammalian olfactory bulb. Depolarizing one system leads to a hyperpolarization in the second system. (iii) One can try to exploit the negative impedance regions in such highly nonlinear systems as the tunnel diode or a Hodgkin-Huxley like membrane.

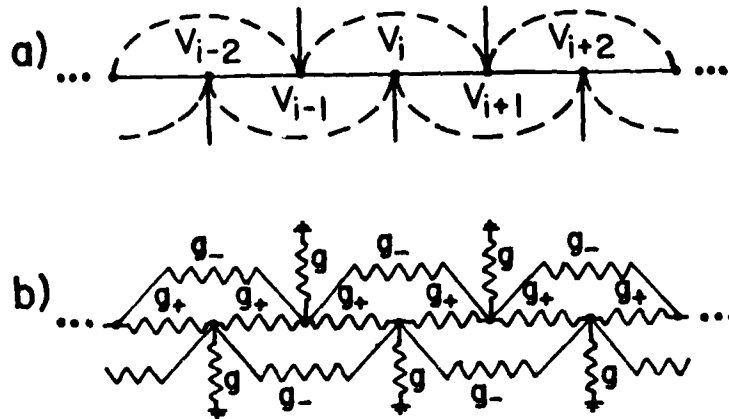


Figure 4: Electrical circuits implementing the regularization solution to edge detection (Poggio et al., 1984; Torre and Poggio, 1984)  $\lambda \frac{d^4 f}{dx^4} + f = y$ . Sampling  $f$  at discrete points  $i$ , we have  $f_{i+2} - 4f_{i+1} + 6f_i - 4f_{i-1} + f_{i-2} + \lambda^{-1} f_i = \lambda^{-1} y_i$ . Fig. 4a shows the topology of the circuit while fig. 4b shows an actual realization. The corresponding network equation is  $g_- V_{i+2} + g_+ V_{i+1} - (2g_+ + 2g_- + g) V_i + g_+ V_{i-1} + g_- V_{i-2} = I_i$ , if  $I_i$  is the current being injected at the  $i$ -th node. The negative resistances  $g_-$  can be implemented using active components. The resistive circuit can, however, be replaced by inductances and capacities and the d.c. voltages and currents by a.c. voltages and currents of fixed frequency<sup>11</sup>.

[12] A regularization analysis of the edge detection problem leads to a simple one-dimensional network that implements the variational equation (1.1). The associated Euler-Lagrange equation is the one-dimensional biharmonic equation  $\frac{d^4 f}{dx^4} = 0$ , where  $f$  is known at some discrete points, i.e.  $f_i = y_i$ , where  $y_i$  is the light intensity. The corresponding electrical network interpolates  $f$  between the sampling points. When the measurements are not exact, the Euler-Lagrange equation is given by  $\lambda \frac{d^4 f}{dx^4} + \sum_i f(x_i) \delta(x - x_i) = \sum_i y_i \delta(x - x_i)$ . The corresponding linear, electrical circuit (fig. 4) approximates  $f$ . Since the corresponding electrical circuits are in both cases space-invariant, the underlying filters are convolution filters (Torre and Poggio, 1984; Poggio et al., 1984).



[13] Two possible chemical and neuronal implementations of the smoothest velocity field computation in the case of non-exact measurements are shown in fig. 5. They correspond to the electrical circuit shown in fig. 1c.

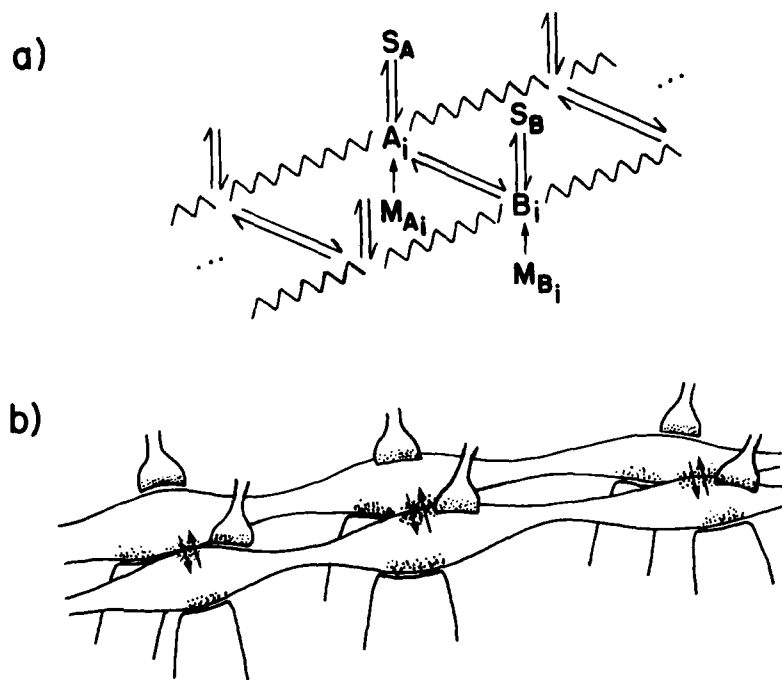


Figure 5: A chemical and a neuronal implementation of equation (11). The cross-term  $c_i$ , which can be negative, is mimicked by either an appropriate non-linear chemical reaction between the two substances  $A_i$  and  $B_i$  or by reciprocal synapses. For the details compare with fig. 2a and 3.

[14] Synapses may implement a variety of linear and nonlinear 1- and 2-ports. A *chemical synapse* converts a presynaptic voltage  $V_{pre}$  into a postsynaptic conductance change  $g_{post}$  (via a chemical process) and corresponds to a non-reciprocal 2-port in the sense of Brayton and Moser (1964) or Oster *et al.* (1971). Its constitutive relation defines a 2-dimensional surface in the four-dimensional space spanned by  $V_{pre}$ ,  $I_{pre}$ ,  $V_{post}$  and  $I_{post}$ . The two presynaptic variables,  $V_{pre}$  and  $I_{pre}$  are related by Ohm's law and similarly for the postsynaptic variables. The relation between  $V_{pre}$  and  $V_{post}$  is given by  $f(x)$ , where  $f$  is in general a nonlinear function. A chemical synapse is non-reciprocal, since variation of any of the two postsynaptic variables does not affect the presynaptic variables. Chemical synapses tend to decouple neuronal systems from each other, rather like operational amplifiers, since a postsynaptic current can be induced without any change in presynaptic current. Depending on  $f$ , synapses can mimic positive or negative resistances. *Reciprocal synapses*, like those found between mitral and granule cells in the olfactory bulb or between bipolar and amacrine cells in the vertebrate retina (Elias and Stevens, 1972), may reintroduce reciprocity. Because  $V_1 = f(V_2)$  and  $V_2 = g(V_1)$ , where  $V_1$  and  $V_2$  are the intracellular voltages of the two neurons,  $V_1$  can be varied while observing its effect on  $V_2$ . Upon reversing the position of observer and input, one expects to obtain symmetrical measurements – at least up to small signals. *Electrical synapses*, usually referred to as gap junctions, provide a low-resistance pathways between cells, thus approximating linear resistances. However, rectifying gap junctions are known to exist, implementing the neuronal equivalent of diodes. The transjunctional resistance can be varied by a variety of neuronal

parameters, such as intracellular calcium concentration, pH and voltage (Bennett, 1972).

[15] The stochastic differential equations describing an electrical or a chemical system with a source of Gaussian noise (for instance voltage or the presence of a chemical reactive substance) can be formulated in terms of Ito or Stratonovitch calculus (Wax, 1954; Gihman and Skorohod, 1972). In physics the equations are called Langevin equations. They can be solved with the Fokker-Planck or the Kolmogorov method. A "solution" of a stochastic differential equation is a characterization in terms of probability distributions of the "output" process. For linear networks, simpler correlation methods can also be used. If the noise is white and Gaussian, its spectral density is proportional to the "temperature"  $T$ . The output is also a Gaussian process with probability distributions that asymptotically approach the Maxwell-Boltzmann distribution.

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